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Feeding ecology of emerald shiners and rainbow smelt in central Lake Erie

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ABSTRACT

To better understand the feeding ecology of two important Laurentian Great Lakes prey species, rainbow smelt *Osmerus mordax* and emerald shiners *Notropis atherinoides*, we quantified the diet composition, selectivity, daily ration, and diet overlap of both species in offshore central Lake Erie during May through October 2005, which spanned a period of severe hypolimnetic hypoxia (<2 mg O₂/L). Rainbow smelt fed upon a variety of prey taxa, including zooplankton, chironomid pupae and larvae, and fish, whereas emerald shiners primarily consumed cladocerans, if available. In turn, diet overlap between rainbow smelt and emerald shiners was low except during September when hypolimnetic hypoxia reduced rainbow smelt access to benthic prey. Rainbow smelt most frequently selected chironomid pupae, while emerald shiners generally selected pupae or large predatory cladocerans (*Leptodora* or *Bythotrephes*). Daily ration and individual consumption by rainbow smelt were 54–68% less during hypoxia than at the same site during stratified pre-hypoxic or mixed post-hypoxic conditions. Although emerald shiner daily ration and individual consumption decreased between pre-hypoxic and hypoxic periods, it continued to decrease during the post-hypoxic period, suggesting that reduced consumption may not have been linked to hypoxic conditions. Ultimately, our findings suggest that emerald shiners are as important regulator of zooplankton abundance in the Great Lakes as rainbow smelt, given their potentially high mass-specific consumption rates, selectivity and diet patterns, and current high abundance.

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Introduction

Planktivorous fishes function both as food for piscivores and as a predator that can influence the composition, abundance, and size structure of zooplankton communities (Brooks 1968, Hartman and Margraf 1992, Johannsson et al. 1999). Although each planktivore species may interact differently with the plankton community (Brooks 1968, Lazzaro 1987, Williams and Moss 2003), a planktivore's role as a predator is sometimes overlooked in favor of describing their role as prey for higher trophic levels (Muth and Busch 1989). To completely assess energy flow in a system and to fully evaluate the impacts of ecosystem disturbances, the feeding ecology of planktivores must be known. Surprisingly, despite the dramatic ecological and food web changes that have taken place in Lake Erie over past decades (Ryan et al. 1999, Ludsin et al. 2001), little historical or

recent data exist on feeding ecology of Lake Erie's major planktivorous fishes, particularly for the central basin, which has the largest area of the three Lake Erie basins and contains nearly two-thirds of the lake's water.

A native planktivore that has persisted in Lake Erie and remains a dominant component of the fish community is the emerald shiner *Notropis atherinoides*, which serves as an important prey for abundant top predators such as walleye *Sander vitreus* (Knight et al. 1984, Knight and Vondracek 1993). Although the emerald shiner can consume benthic macroinvertebrates, it typically consumes cladoceran zooplankton (Ewers 1933, Muth and Busch 1989, Hartman et al. 1992) in the warm epilimnetic waters, where it schools during the daytime and disperses at night (Trautman 1981).

A non-indigenous planktivore that has become a naturalized component of the Lake Erie fish community is the rainbow smelt *Osmerus mordax*. Rainbow smelt invaded Lake Erie during the 1930s and soon became an important component of the ecosystem, supporting both a commercial fishery and piscivore production (Ryan et al. 1999). Rainbow smelt have a broad diet, including zooplankton, macroinvertebrates and small fish, and thus are a potential competitor and predator to other planktivores (Bidgood 1961, Dermott et al. 1999). Unlike emerald shiners, which are a warm-water species, rainbow smelt is a coolwater species that mainly

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confines itself to the hypolimnion and lower metalimnion as an adult (Lantry and Stewart 1993, Dermott et al. 1999, Ryan et al. 1999), which may limit their interactions with other planktivores such as the emerald shiner.

Despite the importance of both rainbow smelt and emerald shiners as prey for top predators in Lake Erie, our understanding of their importance as planktivores in this system remains limited, particularly in the central basin. To better understand 1) how these two species interact and 2) the food web linkages that ultimately support valuable commercial and recreational fisheries for piscivores, we evaluated the feeding ecology of rainbow smelt and emerald shiners in the offshore central basin of Lake Erie, making comparisons with past data collected in other areas of Lake Erie. Offshore waters of the central basin provide a good area to examine interactions between these species because adult rainbow smelt are largely confined to the deeper, offshore waters of this basin over most of the growing season (MacCallum and Regier 1970, Lantry and Stewart 1993). Specifically, we quantified how diets and ration for both species changed with seasonal changes in prey availability, as well as changes in hypolimnetic dissolved oxygen availability, which can potentially reduce fish access to benthic macroinvertebrates and coolwater thermal habitat in the hypolimnion (Aku et al. 1997, Aku and Tonn 1999, Horppila et al. 2000).

Methods

Field sampling

We sampled offshore central Lake Erie during May through October 2005, as part of the International Field Year on Lake Erie (IFYLE) Program (Hawley et al. 2006). Sampling occurred monthly (except during July; no sampling occurred during this month) at a primary site (station B), which is located at the deepest part (~24 m) of the central basin (Fig. 1). To provide greater spatial coverage, samples were taken during some months at additional sites, including station A (June and September) and station H (August) in the western end of the central basin and station D (May, June, August) in the eastern end of the central basin (Fig. 1).

At each site, fish, zooplankton, and physical measurements were collected about every 4-h over a 24-h period. Fish were captured using a 7.6-m semi-balloon bottom trawl (13-mm stretched-mesh cod-liner) and a 9.1 × 9.1-m midwater trawl (6.4-mm stretched-mesh cod-liner). Each trawl was towed for 10 to 20 min along a 5-km transect,

with a minimum of one bottom and one midwater trawl conducted during every 4-h interval. Fish were sorted by species and immediately placed in a freezer.

During each 4-h interval, a Seabird Conductivity, Temperature, Depth (CTD) profiler with an attached YSI oxygen probe was used to provide water-column measurements of temperature and dissolved oxygen availability. Zooplankton were collected at the end points of each 5-km transect at each site aboard a second ship which sampled just ahead of the trawling ship during each 4-h interval. Zooplankton were collected by pumping water with a diaphragm pump from discrete depth zones (epi-, meta-, and hypolimnion), as determined from vertical profiles with the CTD. Water was pumped through a 4-cm diameter hose into a zooplankton net (64-μm mesh) at a rate of 2.0 L/s at 1-m depth intervals within each depth zone so that a total of 1 m³ of water was pumped for each depth zone. After collection, zooplankton were concentrated and transferred to a sample bottle, narcotized with Alka-Seltzer, and preserved with sugar formaldehyde to form a 2% final solution.

Benthic macroinvertebrates were collected at each site once during each 24-h period using a ponar grab (area = 0.047 m²). Triplicate ponar samples were taken at the endpoints and center of the 5-km transect (i.e., 9 total samples per site per 24-h period). Samples were washed through a 0.25-mm nitex mesh net and retained material was preserved with 5% formalin containing rose bengal stain.

Laboratory analyses

To determine zooplankton abundance and composition, an aliquot was taken from a known sample volume with a Hensen-Stempel pipette so that a minimum 550 zooplankters were counted and identified (Brooks 1959, Wilson and Yeatman 1959, Balcer et al. 1984) for each sample. To count large predatory cladocerans (e.g. *Bythotrephes longimanus*, *Leptodora kindti*), that were found in lower densities than other zooplankton, the whole sample was rinsed through a 600-μm mesh sieve and all were identified and counted. Zooplankton densities from the three depth zones were summed to provide a whole water-column density for each time interval and averaged across time periods to provide a single estimate of the available zooplankton community composition and mean density for each site and month.

Macroinvertebrates from ponar samples were placed in a white enamel pan and picked, counted, and identified to family using a low-

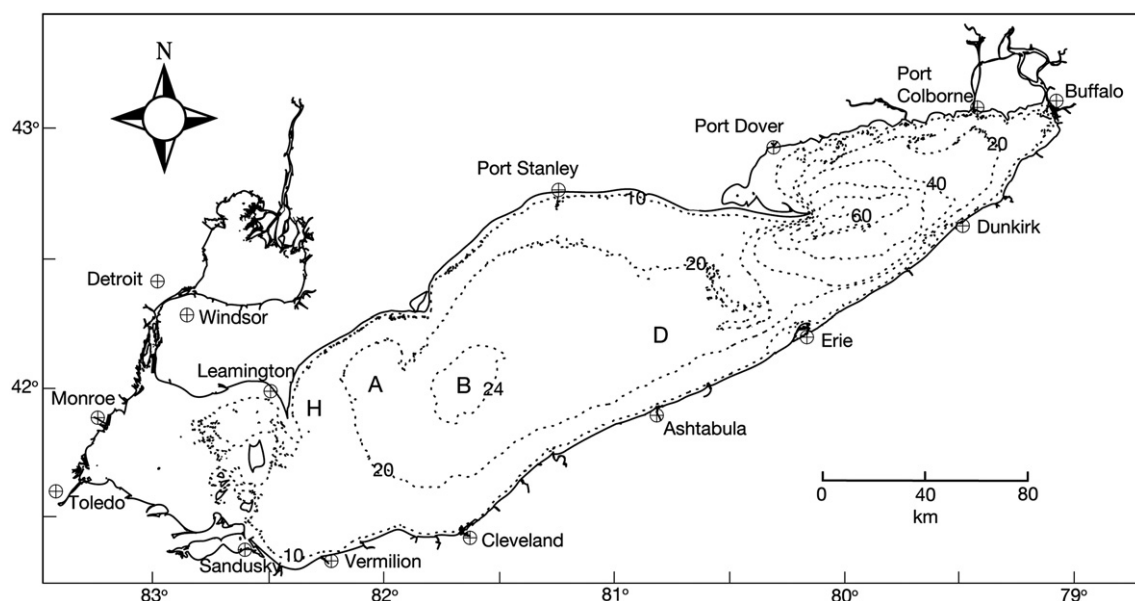


Fig. 1. Location of central Lake Erie stations sampled for this study during May through October 2005. Selected bathymetry lines (depth in m) also are identified.

power magnifier lamp (1.5 x). Chironomidae were further separated into pupae and larvae. The mean density of each macroinvertebrate taxa was determined for each ponar station (i.e., endpoints and midpoint; $n=3$ ponar grabs/station) along each transect and the station means were then averaged ($n=3$ ponar stations/site) to provide a mean macroinvertebrate density for each site and month.

In the laboratory, fish were thawed, measured (nearest 1 mm total length, TL), weighed (nearest 0.01 g wet mass), stomach contents were removed, and the entire fish (minus stomach contents) was dried at 70 °C to a constant mass (nearest 0.0001 g). For rainbow smelt, the stomach contents were determined from the esophagus and stomach; for emerald shiners, which do not have a true stomach, the contents were removed from the esophagus through the second bend in the S-shaped digestive tract (Persson 1982). Stomach contents also were dried at 70 °C to a constant mass after diet composition was determined. Subsamples of fish were taken from larger catches so that for each net haul about 25 individuals of each species with food in their stomachs (if available) were examined during each 4-h interval. For rainbow smelt, only yearling and older (>70 mm) fish were used for analysis because few age-0 fish were caught. For emerald shiners, during August–October, age-0 fish were separated from yearling and older (hereafter adult) emerald shiners based on length frequency distributions. Emerald shiners >70, 75, and 80 mm were classified as adults for August, September, and October respectively. Only adult emerald shiners were collected in May and June.

To determine diet composition, all large prey (e.g. Chironomidae pupae and larvae, *Bythotrephes*, *Leptodora*) from each stomach were identified and counted. Head capsules (Chironomidae) or bodies with eye-spots (*Bythotrephes*, *Leptodora*) were used to count partial prey. Bodies were used to provide a conservative estimate of *Bythotrephes*, because spines can accumulate in stomachs (Parker et al. 2001). Mesozooplankton (e.g., Copepoda, Cladocera) from each stomach were added to a known volume (10–25 mL) of water and sub-sampled with a 1-mL aliquot, so that at least 100 individuals were counted. If stomachs contained fewer than 100 mesozooplankton, all individuals were counted. Mesozooplankton was classified as Bosminidae, Daphniidae, Sidae, Chydoridae, Cyclopoida, Calanoida and nauplii. The number of *Bythotrephes* spines in each stomach was also counted.

From each stomach, prey lengths of up to 20 intact individuals of each prey group (except nauplii) were measured using ImagePro image analysis software (Media Cybernetics, Silver Spring, MD). Prey length was converted to dry mass using mass-length regressions (Culver et al. 1985, Makarewicz and Jones 1990, T. Nalepa and S. Pothoven, unpublished data). The average dry mass of an individual of each prey type was determined for each size class of fish for each site and month and multiplied by the number of each prey type in a stomach to determine dry-biomass contribution of each prey type in an individual stomach. This method of determining diet composition helps correct for different stages of digestion of different prey (Hyslop 1980).

Data analyses

To examine feeding periodicity, the actual measured mass of consumed prey (dry, g food/g fish) was compared across time intervals on each date using a Kruskal–Wallis test. The calculated prey biomass for each prey group was summed across all individual fish from a sample date and site, and diet composition was determined as the percent of the total calculated dry mass. To quantify differences in *Bythotrephes* spine retention between species, which may help to understand any differences in species-specific feeding behavior, the number of spines in a stomach was plotted as a function of the number of *Bythotrephes* bodies for individual fish that contained spines and/or bodies. Slopes of regression lines significantly greater than one would indicate spine retention.

Diet overlap between emerald shiners and rainbow smelt was determined using Spearman's correlation coefficient (r_s), which is a

non-parametric measure of correlation. Prey species that were not consumed in any amount by both fish species at a site for a given month were not used in the correlation analysis. To determine the overall size distribution of zooplankton in diets for both fishes, zooplankton prey were placed into 0.10-mm bins, and the number of each zooplankton prey type (including *Bythotrephes* and *Leptodora*) in a size bin was multiplied by its proportional contribution to the zooplankton component of the diet.

To determine prey selectivity (excluding fish prey), we used Vanderploeg and Scavia's (1979) selectivity coefficient, W' , calculated as:

$$W'_i = (r_i / p_i) / (r_i / p_i)_{\text{pref}} \quad (1)$$

where relative prey abundances in the environment (p) and diet (r) were expressed in numbers and $(r_i / p_i)_{\text{pref}}$ was the maximum value of (r_i / p_i) . Prey abundances were calculated based on the number of each prey in the environment or diet across all time periods for each respective date and site. The selectivity coefficient, W' , varies between 0 (no ingestion of a prey type) to 1, the W' value for the most preferred prey type(s), i.e. the prey type(s) with the maximum value of (r_i / p_i) .

Daily ration was estimated in terms of dry g food/dry g fish/d using the model derived by Eggers (1977),

$$C = F \cdot R \cdot h \quad (2)$$

where C is the consumption rate (g/g/d), F is the average measured dry mass of food in the stomach over the 24-h period (g food/g fish), R is the rate of gastric evacuation (per h), and h is the time in hours of the estimation period (24). We assumed that the same group of fish was sampled over each 24-hour period. We computed F as the mean of the means of each of the six 4-h sample periods because of unequal sample sizes across sample periods (Hayes et al. 1992). The Eggers model was chosen because previous work has shown it to be a robust model that can be used even when assumptions of feeding periodicity or sample frequency are not met (Boisclair and Leggett 1988). Total consumption by an average individual fish (g food/fish/d) was determined by multiplying the daily ration by the average dry mass of an individual fish for a given site and date.

The hourly gastric evacuation rate (R) was determined as the rate at which food was evacuated over a 4-h period as

$$R = (\ln F_{t+4} - \ln F_t) / 4 \quad (3)$$

where F_t and F_{t+4} are mean food mass at the beginning and end of a 4-h time interval. We used the maximum evacuation rate from a diel period for a given day and site for each species to help ensure the likelihood that the assumption of fish not feeding during a given 4-h interval was met. This type of empirical-based approach to evaluate R has commonly been used for planktivorous fishes in field studies (Boisclair and Manchard 1993, Trudel and Boisclair 1994). This approach also did not require us to assume a static foraging temperature, an assumption which is unrealistic when fish vertically migrate.

Results

Physical conditions and prey availability

The water column was stratified at all sites during all months except October, when sampling took place about one week after turnover. Epilimnetic water temperatures were coolest during May and warmest during August (Table 1). While sufficient oxygen was always present in the epilimnion and metalimnion (>7 mg O₂/L), the hypolimnion was hypoxic (<2 mg/L) during August at station H and September at stations A and B (Table 1).

Overall zooplankton abundance was lowest during May and highest during June, with zooplankton abundances being about 4 times higher at stations A and B than at station D during June. The

Table 1

Depth, mean epi-, meta-, and hypolimnetic water temperatures (T), and minimum hypolimnetic dissolved oxygen (O_2) concentration at our sampling sites in the central basin of Lake Erie during May through October 2005.

Site	Depth (m)	Month	Epilimnion T ($^{\circ}\text{C}$)	Metlimnion T ($^{\circ}\text{C}$)	Hypolimnion T ($^{\circ}\text{C}$)	Hypolimnion O_2 (mg/L)
B	24	May	8.4	7.6	6.9	10.4
D	21	May	9.0	8.2	7.9	9.8
A	22	June	18.2	12.6	9.2	8.1
B	24	June	18.2	12.7	8.7	10.3
D	21	June	18.5	11.8	10.0	10.3
B	24	August	25.3	15.4	10.1	4.2
D	21	August	25.5	15.2	13.2	2.8
H	15	August	23.0	14.7	11.8	1.8
A	22	September	21.7	13.3	11.5	0.2
B	24	September	21.9	13.4	11.2	0.3
B	24	October	18.8	18.8	18.8	7.4

zooplankton community (excluding nauplii) was dominated by cyclopoid copepods during May (>90%) and June (71–84%) at all sites (Fig. 2). Zooplankton abundance at station B declined from June to August, with bosminids dominating the community during August (58%) followed by calanoid (28%) and cyclopoid (14%) copepods. Zooplankton composition and abundance at station H during August was similar to station B except that daphnids were more common at station H than at station B (20% vs 4%, respectively). Zooplankton abundance at site D during August was about half that of stations B and H, but was similar to June at the same site. Bosminidae (46%) and calanoid copepods (41%) dominated during August at station D.

During the height of hypoxia in September, zooplankton abundance at station B was slightly higher than during August. Zooplankton abundance was similar between station B and A during September, with cyclopoid copepods (45–46%), calanoid copepods (24–26%), and bosminids (16–20%) dominating samples; other cladocerans (e.g., Daphniidae, Sididae) also were present, but comprised <12% of the community. At station B, zooplankton abundance was lower during October than during September with the community being dominated by cyclopoid (31%) and calanoid (31%) copepods along with daphnids (20%) and bosminids (11%; Fig. 2).

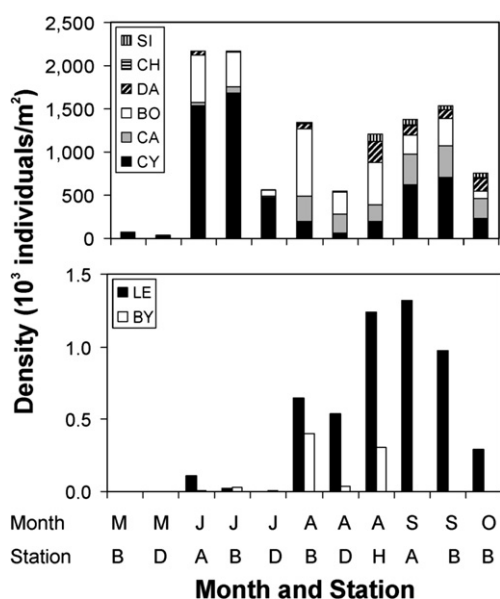


Fig. 2. Whole water-column density (number/m²) of various zooplankton taxa collected during May through October 2005 from central Lake Erie. CY = Cyclopoida, CA = Calanoida, BO = Bosminidae, DA = Daphniidae, CH = Chydoridae, SI = Sididae, LE = *Leptodora*, and BY = *Bythotrephes*. M = May, J = June, A = August, S = September, O = October.

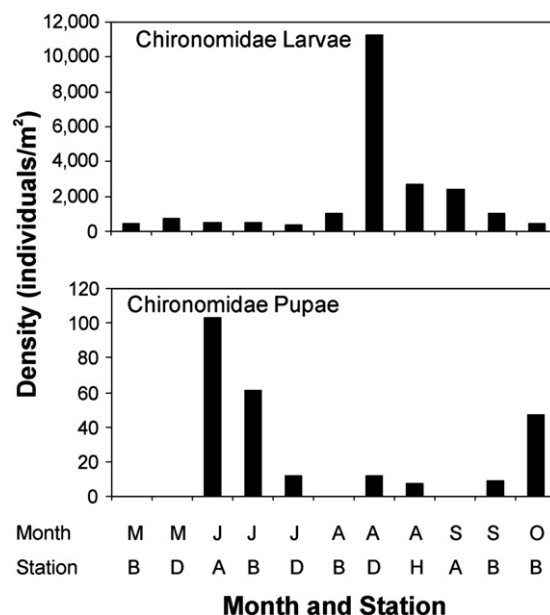


Fig. 3. Density (number/m²) of chironomid larvae and pupae in central basin of Lake Erie during 2005. See Fig. 2 for abbreviations.

Predatory cladocerans *Leptodora* and *Bythotrephes* accounted for a small fraction of the zooplankton community (<1%), with *Leptodora* generally more abundant than *Bythotrephes*. Although present at a site during every sampling month, *Leptodora* density was highest during August and September (Fig. 2). *Bythotrephes* were found at low densities during May and June, densities were highest during August, and they were absent during September and October.

Results for benthic macroinvertebrates are restricted to chironomid larvae and pupae, as chironomids were essentially the only macroinvertebrate consumed by rainbow smelt and emerald shiners.

Table 2

Diet (% dry mass) for adult rainbow smelt (RAS), adult emerald shiners (EMS), and age-0 emerald shiners collected during May through October 2005 at central Lake Erie sampling sites.

Species	% Dry mass of prey
	Site Month CY CA BO DA SI CH LE BY PU LA BE FI n
Adult RAS	B May 85 4 1 2 0 0 0 0 0 7 <1 0 173
	D May 86 2 2 <1 0 <1 0 <1 <1 3 6 0 110
	A June <1 5 1 29 0 <1 <1 0 63 1 <1 0 148
	B June 24 5 1 2 0 <1 <1 63 5 <1 0 197
	D June 1 60 <1 <1 0 0 <1 38 <1 0 0 38
	B Aug 5 3 29 20 <1 1 <1 1 36 4 <1 208
	D Aug 3 32 <1 0 0 15 0 22 6 5 <1 17 71
	H Aug <1 <1 1 50 0 <1 0 <1 <1 0 48 25
	B Sept 3 10 8 17 11 49 1 0 0 0 <1 0 101
	B Oct <1 <1 <1 0 0 <1 1 0 15 0 <1 83 136
Adult EMS	B May 77 0 0 0 0 0 0 0 2 20 0 0 61
	A June <1 <1 3 34 0 0 0 0 63 0 0 0 32
	B Aug 0 0 2 <1 0 0 12 87 0 0 0 0 22
	D Aug 0 0 <1 0 0 0 0 8 92 0 0 0 18
	H Aug <1 <1 1 27 <1 33 34 0 0 0 0 33
	A Sep 1 <1 20 24 48 <1 6 0 0 0 0 0 75
	B Sep 1 1 14 8 61 <1 13 0 0 0 0 0 40
	B Oct <1 1 <1 3 <1 4 0 85 6 <1 0 92
	B Aug <1 2 43 6 0 <1 2 47 0 0 0 0 66
	D Aug 1 2 32 <1 <1 0 4 22 39 0 0 0 64
Age-0 EMS	H Aug <1 <1 52 17 <1 0 2 30 0 0 0 72
	A Sep 1 <1 21 11 61 <1 3 <1 0 0 0 0 96
	B Sep 4 6 44 4 36 1 <1 0 0 0 0 107
	B Oct <1 <1 1 4 <1 0 1 0 95 0 <1 0 107

Prey types: CY = Cyclopoida, CA = Calanoida, BO = Bosminidae, DA = Daphniidae, SI = Sididae, CH = Chydoridae, LE = *Leptodora*, BY = *Bythotrephes*, PU = chironomid pupae, LA = chironomid larvae, BE = other benthos, including Oligochaeta, Isopoda, Mollusca, Ostracoda, FI = fish; n = number of fish with food in their stomachs.

Abundance of chironomid larvae was highest during August and September, with lower numbers during May, June, and October (Fig. 3). Chironomid pupae were much less abundant than larvae with peak densities of between 61 individuals/m² and 103/m² observed during June (stations A and B) and October, and lower densities (<12/m²) found at all other sites and months.

Planktivore diets

The diets of 1498 adult rainbow smelt, 513 adult emerald shiners, and 746 age-0 emerald shiners were quantified for this study. Rainbow smelt and emerald shiners were the main planktivores collected from the central basin, accounting for 57% and 22% of the total trawl catch by number, respectively. Yellow perch *Perca flavescens*, a benthivore, was the only other fish species collected in high abundance at our sampling sites (18% of catch). Based on TL distributions, most rainbow smelt were age-2 or older, with average TLs (by month) ranging between 110 mm (May) and 135 mm (October). Adult emerald shiners' TLs averaged 81 to 92 mm over the course of the study, and age-0 emerald shiners averaged 54 to 64 mm TL during August to October.

Both rainbow smelt and emerald shiner diets varied by month and site (Table 2). During May, rainbow smelt consumed mainly cyclopoid copepods at both stations B (85%) and D (86%) (Table 2). During June, chironomid pupae comprised 38–63% of the diet at each of the three sites sampled, and zooplankton comprised the bulk of the remaining diet. However, the zooplankton contributing to the diet in June varied

by site, with calanoid copepods being most important at station D, cyclopoid copepods being most important at station B, and Daphnidae being most important at station A. During August, rainbow smelt diets differed among the three sites sampled: 1) at station B, Daphnidae, Bosminidae, and chironomid larvae all contributed at least 20% to the diet; 2) at station D, diets were dominated by calanoid copepods (32%), *Bythotrephes* (22%), and fish (17%); and 3) at station H, Daphnidae (50%) and fish (48%) dominated rainbow smelt diets. Because too few rainbow smelt were collected for analysis at station A during September, data were only available for station B during this month. At this time at station B, rainbow smelt did not consume chironomids, feeding mainly on cladocerans including Chydoridae (49%), Daphnidae (17%), and Sididae (11%). During October, mainly fish (83%) and chironomid pupae (15%) were consumed and the most common zooplankton taxon in rainbow smelt diets was *Leptodora* (1%). Most fish consumed by rainbow smelt were age-0 emerald shiners or rainbow smelt.

During May and June, emerald shiners were only caught in sufficient numbers for analysis at stations B (May) and A (June). During May, cyclopoid copepods (77%) and chironomid larvae (20%) were primarily consumed (Table 2). During June, chironomid pupae dominated diets (63%) with Daphnidae (34%) also being consumed to a high degree. During August, Bosminidae and *Bythotrephes* made significant contributions (22–52%) to the diet of age-0 emerald shiners at the three sites sampled, along with chironomid pupae at station D, and Daphnidae at station H. During August, the diet of adult emerald shiners varied by site: 1) chironomid pupae (92%) dominated

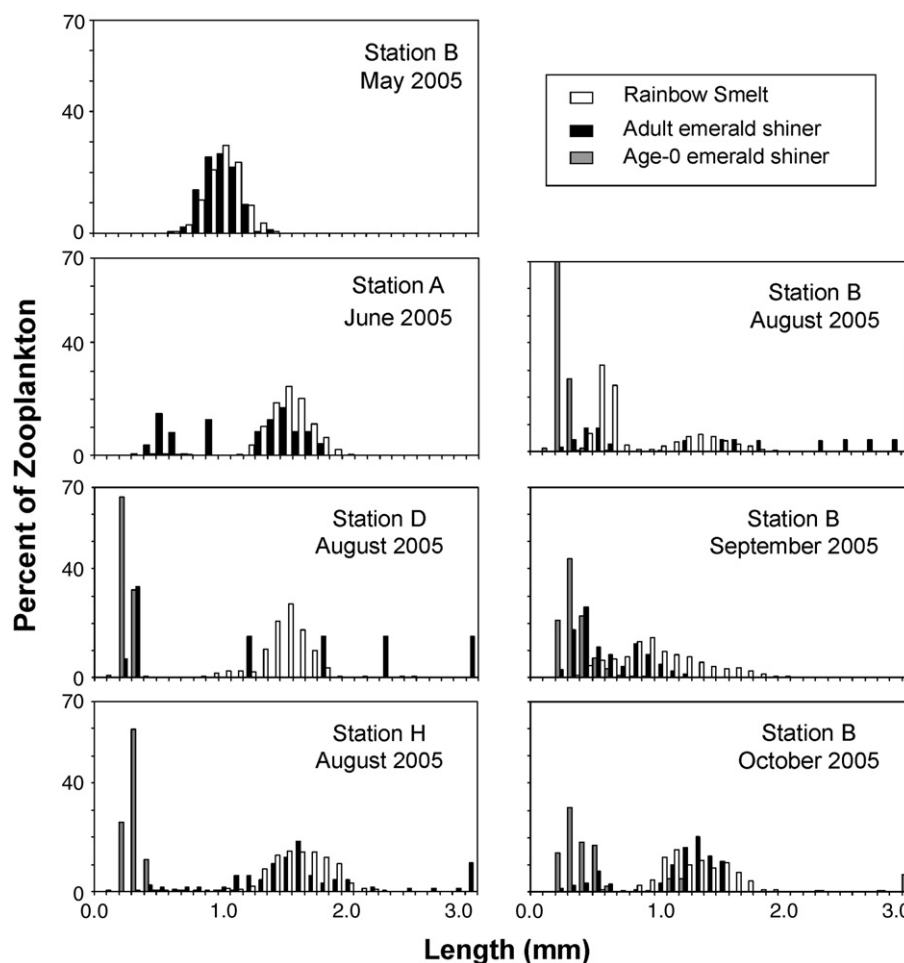


Fig. 4. Size distribution of zooplankton in diets of adult rainbow smelt, adult emerald shiners, and age-0 emerald shiners during 2005 in central Lake Erie. Distributions shown only for months and sites when both rainbow smelt and emerald shiners were collected.

diets at station D; 2) *Bythotrephes* (87%) were consumed to a high degree at station B; and 3) a combination *Daphnidae*, *Leptodora*, and *Bythotrephes* were consumed at station H. During the height of hypoxia in September at stations A and B, the diets of both age-0 and adult emerald shiners were dominated by cladocerans (83–93%), primarily *Sididae* and *Bosminidae*. During October, chironomid pupae dominated the diets of age-0 and adult emerald shiners (>85%).

The slope of the linear regression line relating the number of *Bythotrephes* spines as a function of the number of *Bythotrephes* bodies in a rainbow smelt stomach was 0.94 (0.78–1.11, 95% CI, $n = 167$), indicating that spines did not accumulate in stomachs. By contrast, the slope was 0.14 (0.10–0.18, 95% CI, $n = 138$) for emerald shiners, indicating that fewer spines were in stomachs than expected. In fact, only 19 *Bythotrephes* spines were found in emerald shiner stomachs as compared to 137 bodies.

Diet overlap

Correlation among ranked diet items for rainbow smelt and emerald shiners was only significant during September at station B ($r_s = 0.62$, $n = 12$, $P < 0.05$). The size distributions of zooplankton in diets were similar between adult emerald shiners and rainbow smelt during May (Fig. 4). During other months however, adult emerald shiners tended to consume a wider size range of zooplankton than rainbow smelt. Age-0 emerald shiners generally consumed smaller zooplankton than either adult emerald shiners or rainbow smelt; however during October, their diets also included a substantial proportion of the largest zooplankton.

Selectivity

May was the only month during which copepods were selected by either species (i.e. $W' = 1$), with calanoid copepods selected by rainbow smelt and cyclopoid copepods by emerald shiners (Fig. 5). Rainbow smelt selected chironomid pupae at all other sites except station B during September, at which time chydorids were selected. Emerald shiners (adults and age-0) selected chironomid pupae at station A during June, station D during August and station B during October, but selected *Leptodora* or *Bythotrephes* at stations B and H during August and station B during September.

Daily ration

Diel feeding patterns were evident for both species with stomach biomass varying among 4-h time blocks at each site during each month (all $P < 0.01$). Stomach biomass was generally lowest at night and/or early morning (0100–0700 samples) for rainbow smelt for a given site during each sample effort, although we observed some variation in patterns across months (Fig. 6). A similar, but more distinct, diel feeding pattern was observed for emerald shiners as compared to rainbow smelt (Fig. 6). Emerald shiner stomach biomass was greatest during late day (1400–2100) and was generally lowest at night, except during October, when stomach biomass was highest at night and into the early morning (0300–1100).

Daily ration (g/g/d) for rainbow smelt varied considerably across months. On average, it increased from May to its highest level during June, decreased June to August, declined further from August to its

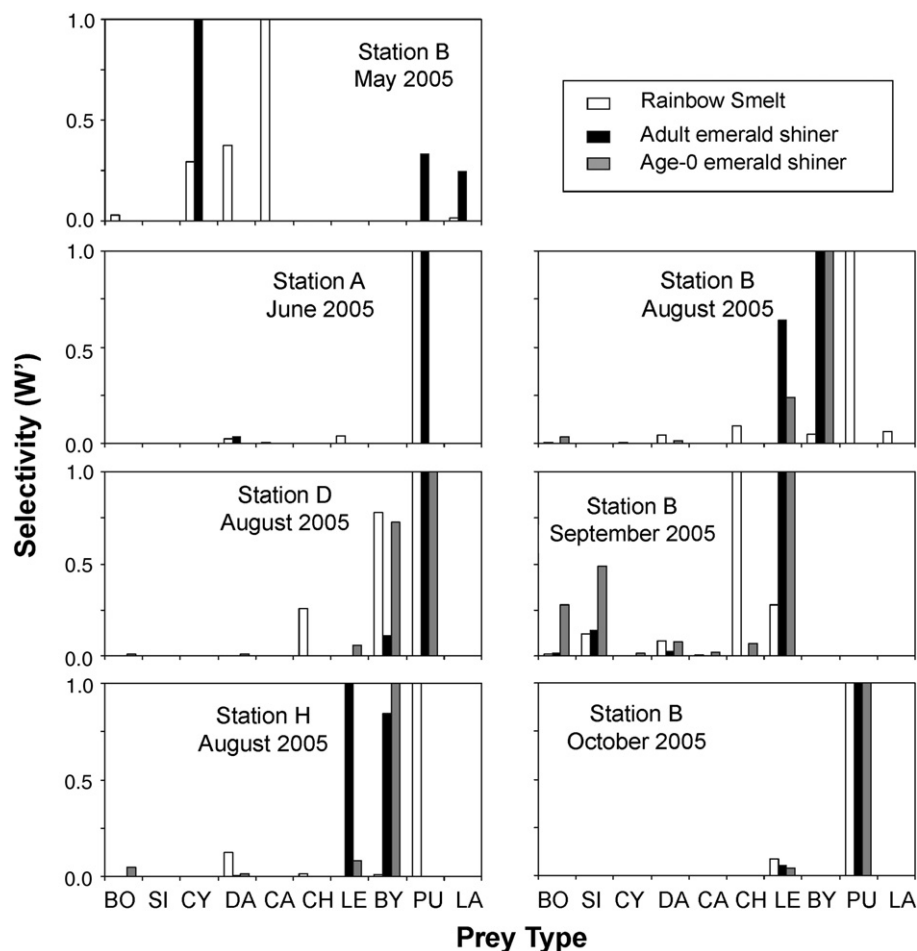


Fig. 5. Prey selectivity (W') by rainbow smelt and adult and age-0 emerald shiners during 2005 in central Lake Erie. Selectivity shown only for months and sites when both rainbow smelt and emerald shiners were collected. Prey listed in order of increasing size from left to right. PU = pupae, LA = larvae, see Fig. 2 for other abbreviations.

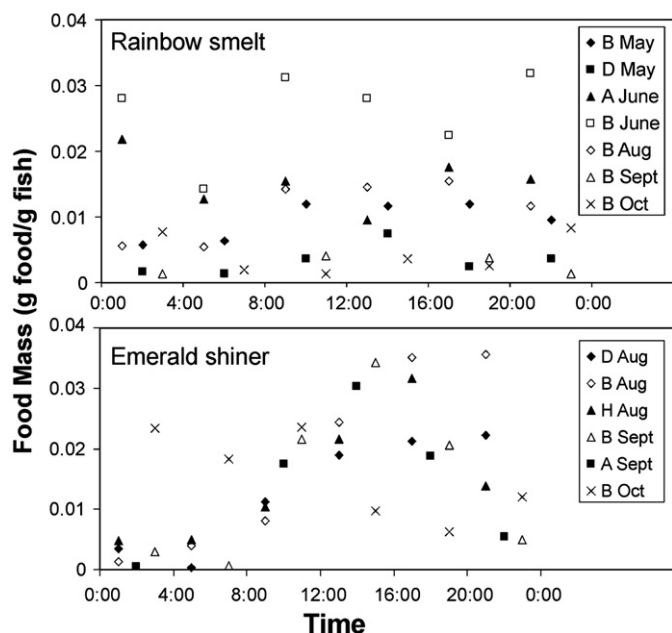


Fig. 6. Stomach content biomass (dry, g food/g fish) over a 24-h cycle for rainbow smelt and emerald shiners at four stations in central Lake Erie during May–October, 2005.

lowest level in September, and then increased from September to October (Fig. 7). Individual consumption (g/fish/d) for an average rainbow smelt was lowest during May (0.021 to 0.034 g/fish/d) and September (0.051 g/fish/d) as compared to June, August, and October (0.098 to 0.161 g/fish/d).

Ration could not be determined for emerald shiners for May and June due to small sample sizes for some time periods. Daily ration decreased on average from 0.21 g/g/d in August to 0.16 g/g/d in September to 0.08 g/g/d in October, but there was considerable variation across sites for a given month (Fig. 7). Individual consumption was similar on average between August and September (0.10 g/fish/d), but lower in October (0.05 g/fish/d), but as with daily ration, there was considerable variation across sites for a given month. Emerald shiner daily ration averaged 0.27 and 0.14 g/g/d for stratified, non-hypoxic sites as compared to hypoxic sites during August and September, respectively; individual consumption averaged 0.11 and 0.09 g/fish/d at the same sites. During August and October, individual consumption by rainbow smelt was higher than that of an average emerald shiner, but in September, individual consumption by emerald shiners was higher than rainbow smelt (Fig. 7).

Discussion

Similar to previous studies within the Laurentian Great Lakes, including Lake Erie, central basin rainbow smelt consumed a variety of prey including zooplankton, benthic macroinvertebrates, and fish. Previous work in the deeper eastern basin of Lake Erie demonstrated that rainbow smelt undergo ontogenetic diet shifts from small zooplankton to large zooplankton to macroinvertebrates and fish as they increase in size (Bidgood 1961). Our central Lake Erie data indicate that similar prey shifts also can occur over the year within a single size group of adult fish, with seasonal changes in diet reflecting changes in prey availability. For example, during May cyclopoid copepods were the most abundant prey item available in the ambient environment and dominated rainbow smelt diets; however, as summer progressed, cladocerans generally increased in the environment and became more prevalent in their diets. Peaks in chironomid pupae in the diet during June and October also corresponded with high relative abundances in the environment. The importance of fish in diets during late summer and early fall at some sites likely reflects

the relative availability of age-0 fish (e.g., emerald shiners) at this time, as age-0 fish were not collected in survey gear until late summer in central Lake Erie (S. Ludsins, unpublished data).

Bidgood (1961) indicated that progressively larger prey were important for efficient growth of rainbow smelt in Lake Erie. In lakes Michigan, Superior, and Huron, large prey including *Mysis relicta*, *Diporeia* spp., Ephemeroptera, Diptera, or fish also have been shown to be important prey for rainbow smelt (Gordon 1961, Crowder et al. 1981, Johnson et al. 2004, Hondorp et al. 2005). In eastern Lake Erie, the decline of the amphipod *Diporeia* was suggested as one factor contributing to declines in rainbow smelt growth (Dermott et al. 1999). In the central basin of Lake Erie, however, *Diporeia* have historically been rare (Bidgood 1961, Dermott et al. 1999), and rainbow smelt likely have always selected and exploited ephemeral or benthic prey such as chironomid pupae and larvae.

Previous diet studies conducted on rainbow smelt in eastern Lake Erie have demonstrated a shift from reliance on cladocerans during the 1960s to calanoid copepods and emergent insects during the mid to late 1990s (Dermott et al. 1999, Parker-Stetter et al. 2005). In the central basin, however, cladocerans remain an important prey item (>50% of diet) during the summer at our stations, with the exception of our easternmost site (station D), where calanoid copepods were an important prey item during both spring and summer. The importance of calanoid copepods at station D reflected their high relative abundance coupled with low abundance of cladocerans.

In contrast to rainbow smelt, previous diet analyses of Lake Erie emerald shiners have focused on the west basin. Most data from summer to early fall (June to October) indicate that cladocerans have historically been the main prey for emerald shiners in the west basin (Muth and Busch 1989, Hartman et al. 1992), although a limited data set from April 1929 indicates that emerald shiners can consume copepods and chironomid pupae during early spring (Ewers 1933). Similarly, we found a strong reliance on several genera of cladocerans by both adult and age-0 emerald shiners in the central basin. In fact, other than May, when cladocerans were essentially absent in the environment, copepods generally comprised <3% of emerald shiner diets. In addition to cladocerans, we also noted the occasional selection

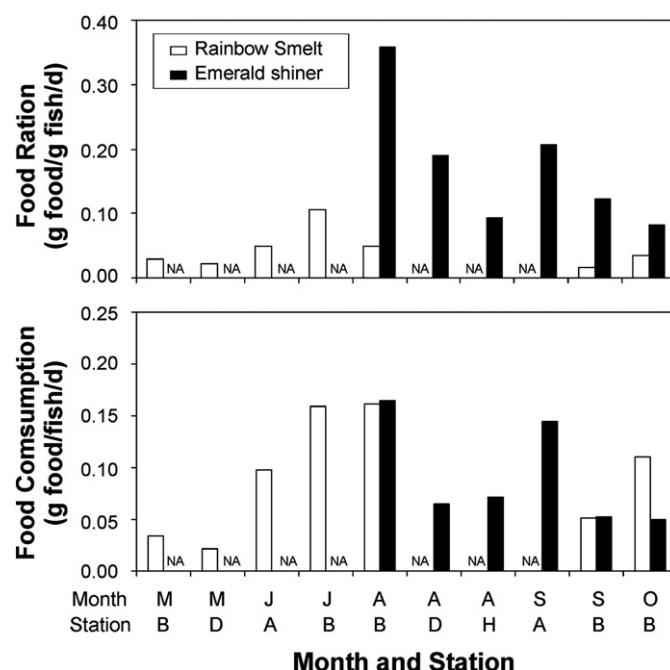


Fig. 7. Daily ration (g food/g fish/d, dry mass; top panel) and daily individual consumption (g food/fish/d, dry mass; bottom panel) for rainbow smelt and emerald shiners in central Lake Erie during May through October 2005. NA = not available. See Fig. 2 for abbreviations.

and importance of chironomid pupae in emerald shiner diets. A study of emerald shiner diets in a South Dakota, U.S.A. reservoir indicated that, although emerald shiners do prefer large-bodied cladocerans, they also prey upon insects and are capable of consuming large, ephemeral prey (Fuchs 1967). In contrast to rainbow smelt, however, chironomid larvae were generally absent from emerald shiner diets, likely owing to emerald shiner's epilimnetic distribution.

The predatory cladoceran, *B. longimanus* has been a persistent component of the zooplankton community in central Lake Erie since the late 1980s and, if abundant, may consume as much as 31–64% of the summer zooplankton production (Johannsson et al. 1999). Although rainbow smelt consumed *Bythotrephes* when available (mainly in August), *Bythotrephes* accounted for a much larger proportion of the diets of both age-0 and adult emerald shiners during the same period. This finding was a bit unexpected, as *Bythotrephes* has a long tail spine which is believed to inhibit small fish from eating them (Barnhisel and Harvey 1995). In fact, we found that emerald shiners as small as 42 mm (and rainbow smelt as small as 58 mm) could consume *Bythotrephes*. Interestingly, foraging on *Bythotrephes* is believed to have contributed to slower growth rates of rainbow smelt in eastern Lake Erie, owing to retention of non-digestible spines in the stomach (Parker-Stetter et al. 2005). However, neither rainbow smelt nor emerald shiners appeared to retain spines in this study. In fact, almost no spines were found in emerald shiner stomachs despite the importance of *Bythotrephes* as a prey item. Other studies have noted species-specific differences in retention of *Bythotrephes* spines related to gut design, feeding mode, or how prey are handled before ingestion (Branstrator and Lehman 1996, Coulas et al. 1998).

We found that both rainbow smelt and emerald shiners tended to forage during daylight hours, similar to some other small-bodied planktivores, such as the bay anchovy *Anchoa mitchilli* (Hartman et al. 2004). In contrast, some planktivores in the Great Lakes such as the alewife *Alosa pseudoharengus* feed during both day and night (Janssen et al. 1995). Ultimately, our finding are important because they suggest that efforts to model consumption for rainbow smelt and emerald shiners need only focus on prey availability and foraging during daylight or crepuscular periods.

The likelihood of direct inter-specific competition between rainbow smelt and emerald shiners in central Lake Erie appeared to be low. During May, owing to a smaller difference in average epilimnetic and hypolimnetic temperature relative to other months, physical overlap of both species in the water column could be higher than during other months. At this time, similar prey types and sizes were consumed, but correlation among ranked diet items was low. After May, diet overlap was generally low. And, owing to species-specific thermal preferences, spatial segregation appeared to occur with rainbow smelt occupying the cooler metalimnion or hypolimnion and emerald shiners occupying the warm epilimnion, as has been documented elsewhere (MacCallum and Regier 1970, Trautman 1981, Lantry and Stewart 1993). We did observe a significant correlation of ranked diet items during September at station B, a period when hypoxia reduced rainbow smelt access to benthic prey; but the size distributions of prey differed between species, thus reducing potential overlap. Whether abundances and consumption rates of adult rainbow smelt and emerald shiners were high enough to competitively affect each other remains unknown.

Seasonal hypolimnetic hypoxia is a natural, long-standing phenomenon in the central basin of Lake Erie that has been exacerbated in the past by cultural eutrophication (Charlton 1987, Bertram 1993), and was particularly problematic during 2005 (Hawley et al. 2006). Fish acoustics and trawl data collected along with our diet data demonstrate that hypoxia (<2 mg O₂/L) likely forced rainbow smelt to reside in a 1–2 m band of water above the oxycline (i.e., at the metalimnetic oxycline; S. Ludsins, unpublished data). Similar findings have been found in other systems. For example, smelt *Osmerus eperlanus* in a Finnish lake remained in unfavorably warm water to

avoid crossing a strong oxygen gradient, providing phantom midge larvae *Chaoborus* a refuge in the low oxygen water (Horppila et al. 2000). Likewise, bay anchovy in the Neuse River Estuary aggregate at the pycnocline (just above hypoxic sub-pycnocline waters), where they cannot access large supplies of copepod zooplankton below the pycnocline (Taylor and Rand 2003).

Reduced access to hypoxic bottom waters is likely responsible for the lack of benthic prey such as chironomid larvae in rainbow smelt diets. At hypoxic sites at which rainbow smelt were collected, individuals only consumed zooplankton (station B, September) or zooplankton and fish (station H, August). Additionally, daily ration and individual consumption were each 68% less when the hypolimnion was hypoxic than at the same site during stratified conditions without hypoxia, even though temperatures were similar and zooplankton abundance was slightly higher during the hypoxic sample period. The decline in consumption for rainbow smelt was largely related to the loss of benthic prey in the diets and secondarily to lower amounts of zooplankton eaten. Ration for rainbow smelt rebounded during the post-hypoxic sampling in October.

Although emerald shiner daily ration and individual consumption declined between the pre-hypoxic and hypoxic periods, it continued to decrease during the post-hypoxic period, suggesting that reduced consumption may not have been linked to hypoxic conditions. Emerald shiners do not normally occupy hypolimnetic waters or rely on benthic prey. As such, hypoxia may have less negative impact on the feeding ecology of emerald shiners than rainbow smelt. Additionally, unlike the Neuse River Estuary where the hypoxic zone can serve as a refuge for zooplankton (Taylor and Rand 2003), zooplankton in Lake Erie tend to avoid severe hypoxia by aggregating in the water column at or just above the oxycline/metalimnion (H. Vanderploeg pers. comm.). In this way, hypoxia actually may enhance access to zooplankton prey for emerald shiners. Further, although hypoxia-induced changes in rainbow smelt feeding and distribution, such as increased use of metalimnetic waters and zooplankton prey, could potentially negatively affect emerald shiners through indirect pathways (i.e., competition for zooplankton resources), differences in selectivity and zooplankton size distributions in diets between species suggest otherwise. Most certainly, more research is needed to better understand how hypoxia mediates interactions amongst rainbow smelt, emerald shiners, and their prey.

Emerald shiners appear as likely as rainbow smelt to influence zooplankton community structure and abundance in central Lake Erie, given their relatively high mass-specific consumption rates, a diet consisting mainly of cladoceran zooplankton, and selection for large predatory cladocerans. Given the feeding patterns and consumption rates for emerald shiners, combined with their current high relative abundance in central Lake Erie as compared to rainbow smelt (Ohio Division of Wildlife, 2007), it is clear that this species needs to be accounted for in food web analyses of planktivory. Similarly, Klumb et al. (2004) suggested that emerald shiners are functionally equivalent to alewife with regard to zooplankton predation in Lake Ontario and should be considered a strong regulator of zooplankton size and species composition.

Our results indicate that rainbow smelt and emerald shiners function differently as predators on zooplankton and invertebrate prey communities in central Lake Erie. Ongoing ecological changes occurring in the central basin, including oligotrophication (Ludsins et al. 2001), the proliferation of invasive species that may ultimately reduce zooplankton abundance and community structure (Johannsson et al. 1999), and increasing hypoxia (Hawley et al. 2006) will likely affect each of these species differently. In turn, owing to differing diets, prey selectivity patterns, and daily rations between species, high abundance of either (or both) of these species has differing potential to alter zooplankton community composition, biomass, and production. Such changes then could influence the potential capacity of the system to support forage fish production and ultimately piscivore production through bottom-up processes, as well potentially influence the success

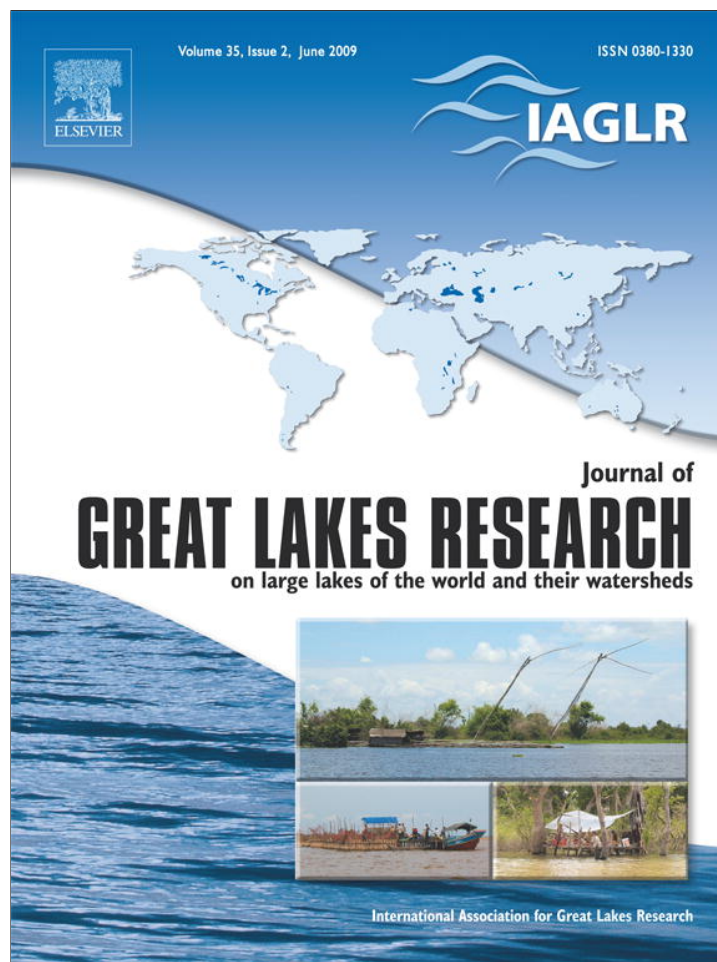
of extant and future invasive species or even the suitability of the central basin ecosystem for recovery of native fish species such as lake herring *Coregonus artedii*. For these reasons, we encourage continued research to better understand the role of planktivorous fishes, such as rainbow smelt and emerald shiners in the Great Lakes.

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